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Development and life cycles

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Development and life cycles

Gerald D. Schmidt

8.1 Introduction

Embryological development and biology of the Acanthocephala occupied the attention of several early investigators. Most notable among these were Leuckart (1862), Schneider (1871), Hamann (1891 *a*) and Kaiser (1893). These works and others, including his own observations, were summarized by Meyer (1933) in the monograph celebrated by the present volume. For this reason findings of these early researchers are not discussed further, except to say that it would be difficult to find more elegant, detailed and correct studies of acanthocephalan ontogeny than those published by these pioneers.

Since Meyer's monograph, many studies have been published on most aspects of the biology of the Acanthocephala. When comparing these, recurring patterns in development are observed. A discussion of these patterns is the main content of this chapter. The postzygotic development of the acanthor, acanthella and cystacanth stages are described first, followed by examples from the three classes, Archiacanthocephala, Palaeacanthocephala and Eoacanthocephala. Finally, a table of all post-1932 literature references to intermediate and paratenic hosts that I have been able to find is presented.

8.2 Postzygotic development

8.2.1 *Acanthor*

Following fertilization and reorganization of the zygote, described in the previous chapter, cell division begins the formation of the acanthor, the stage in the life cycle that is infective to the intermediate host. The first published study of this early embryology, that of Hamann (1891 *a*), remains the definitive work on general acanthocephalan embryology to this day (Schmidt, 1973 *b*). In this landmark paper Hamann clearly

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demonstrated the early embryology of *Acanthocephalus ranae*, and *Echinorhynchus gadi*, both in the class Palaeacanthocephala. Nicholas & Hynes (1963*b*) studied *Polymorphus minutus*, also a palaeacanthocephalan.

In the Eoacanthocephala, Meyer (1931*a*) studied *Neoechinorhynchus rutili*, the only investigation so far reported for this class.

In the Archiacanthocephala, Meyer (1928, 1937, 1938*a, b*) studied *Macracanthorhynchus hirudinaceus*, and Nicholas (1967, 1973) worked with *Moniliformis moniliformis*. Schmidt (1973*b*) described the developing acanthor of *Mediorhynchus grandis*.

Thus, examples from all three classes of Acanthocephala have been examined and can be compared.

Cell division begins and continues while the embryo is still attached to the ovarian ball. The diploid number varies among species from 5 to 16 (Parshad & Crompton, 1981). Polar bodies can be seen as two darkly staining spheres at one end of the embryo (Fig. 8.1). The polar bodies mark the future anterior end of the animal, which is opposite to the condition known for other phyla. This is one of the two unusual aspects of polarity seen in the development of Acanthocephala.

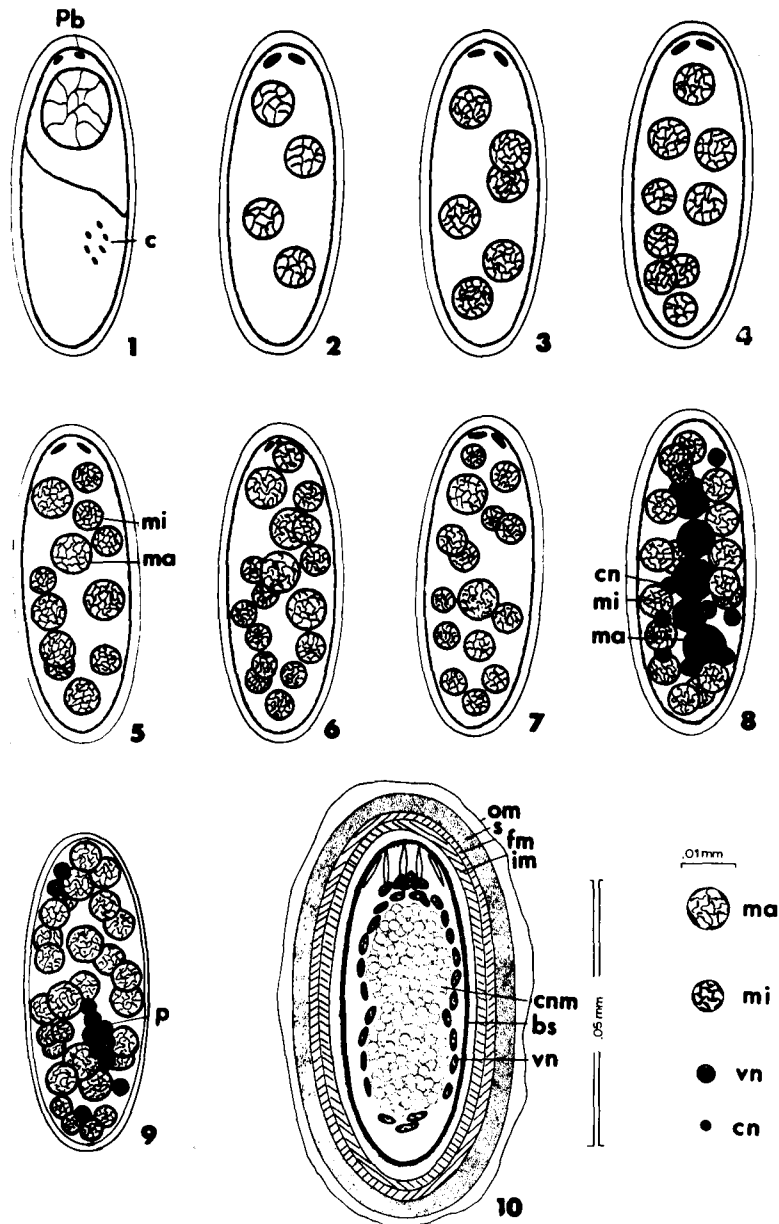
The first division forms two blastomeres of about equal size, the nuclei of which lie one behind the other along the long axis of the embryo. Second divisions occur rapidly with approximately equal blastomere nuclei arranging in a spiral around the axis. Meyer (1936) considered acanthocephalan cleavage to be a distortion of typical spiral cleavage, and even considered that of *M. hirudinaceus* to be determinate, exhibiting the 4D origin of the mesoderm. It is not clear whether this conclusion is justified.

The first four cells are equal in size in all species studied except for *N. rutili* where the posterior cell, called D by Meyer (1931*a*), is larger and denser than the others.

Fig. 8.1. Early embryology of *Mediorhynchus grandis*. 1, Two cell stage. Prophase of division of posterior blastomere. 2, Four-nuclei stage, showing spiral cleavage and absence of apparent cell membranes. 3, Six-nuclei stage. 4, Nine-nuclei stage, with posterior quadrant of micromeres. 5, Twelve-nuclei stage. 6–7, Macromeres and micromeres, showing anterior quadrant of micromeres (some nuclei omitted). 8, Formation of condensed nuclei. 9, Inward migration of condensed nuclei, forming primordium of central nuclear mass. 10, Mature acanthor, with enclosing membranes (diagrammatic). bs, body spines; c, chromosomes; cn, condensed nucleus; cnm, central nuclear mass; fm, fertilization membrane; im, inner membrane; ma, macromere; mi, micromere; om, outer membrane; p, primordium of central nuclear mass; Pb, polar bodies; s, second membrane; vn, vesicular nucleus. (From Schmidt, 1973*b*.)

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The body of the embryo becomes a syncytium which remains throughout the life of the worm. The loss of cell membranes may occur as early as the four-cell stage, in the case of *M. grandis*, or 36-cell stage in *P. minutus* and *M. hirudinaceus*. Hamann (1891*a*) did not mention the disappearance of cell membranes in the species he studied. In fact, he illustrated their presence in all stages leading to the complete acanthor. It seems improbable that he actually saw such membranes when later workers were unable to do so. Yet, Nicholas (1973) indicated that preliminary electron microscopical studies suggested that cell membranes actually do persist throughout the early stages. I doubt that they do, but I am reluctant to discount Hamann as having a too active imagination.

Subsequent nuclear divisions are unequal, with micromeres (small nuclei) accumulating as quartets at the poles, then becoming randomly dispersed. Four macromeres (large nuclei) remain near the central axis, giving rise to micromeres. The embryo at this time may be called a stereoblastula.

As cleavage continues, macromeres can no longer be identified. The polar bodies disappear at about the 18- to 36-nuclei stage, but their lack of proximity to the last discernible macronucleus indicates that they are at the future anterior end of the acanthor (Nicholas & Hynes, 1963*a*).

While some nuclei continue to divide, most contract into tiny, dense bodies which begin migrating inward to form the central nuclear mass, or mesoderm. This mass develops into all of the adult structures except the tegument and lemnisci. The nuclear migration is considered a form of gastrulation, and the embryo can be considered a stereogastrula. A number of vesicular nuclei remain in the cortex of the embryo, to become the nuclear components of the tegument and lemnisci. By this time the embryo has detached from the ovarian ball.

Organogenesis proceeds rapidly. The syncytial body mass is divided into cortical and medullary regions, with the nuclear mass girdling the constricted, central medulla. It is along the junction of these two regions that a split occurs later, forming the pseudocoel.

A small, ventral or terminal depression develops at the anterior end of the embryo. Known as the aclid organ it is the boring mechanism with which the fully developed larva penetrates the gut of its intermediate host. It is bordered by spines that aid in the cutting process. Internal contractile fibers originate on the inner surface of the aclid organ and insert somewhere internally; exactly where is not known. When these fibers contract, the aclid organ is pulled inward, which points the spines anteriorly. Upon relaxation of the fibers the organ snaps back into place, causing the spines to have a sweeping, cutting action. Acclid organ spines vary

considerably in number, size and arrangement among species. For a review see Grabda-Kazubska (1964). They are said to be absent in the eoacanthocephalan genus *Neoechinorhynchus*, but Hopp (1954) observed minute spines on the acanthor of *N. emydis*. They may, in fact, be present in all. Most species have additional circles of spines over most of the body surface. Acanthor spines persist on the acanthella and often have been seen late in the development of the worm.

By the time the embryo has developed as described above, it has also surrounded itself with a series of envelopes, or membranes. Differences in the number of membranes can be found in the literature, with most authors describing three or four. The subject was admirably discussed by Whitfield (1973) who demonstrated electron microscopically that there are three in *Polymorphus minutus*. The outermost envelope probably is the fertilization membrane. The next inner membrane is comprised of two layers, which may account for the reports of a total of four layers. Closely investing the acanthor is the innermost envelope. Only 20–30 nm thick it cannot be seen with the light microscope, except that when the acanthor is observed while hatching a displacement of surrounding fluids clearly outlines its presence. Whitfield's paper should be consulted for further structural and compositional features of the egg membranes.

Further development cannot occur until the acanthor, enclosed within its membranes, exits its mother's genital pore to be swept out of the definitive host along with other intestinal contents. Then it must be eaten by the proper intermediate host, where it hatches in the intestine. Mechanisms of hatching have been studied by Edmonds (1966).

Without a known exception the first intermediate hosts of acanthocephalans are arthropods, either a crustacean in aquatic species or an insect (or rarely a myriopod) in terrestrial species (see Table 8.1). Reports of cystacanths in other invertebrates, such as snails or annelids probably represent accidental or paratenic hosts.

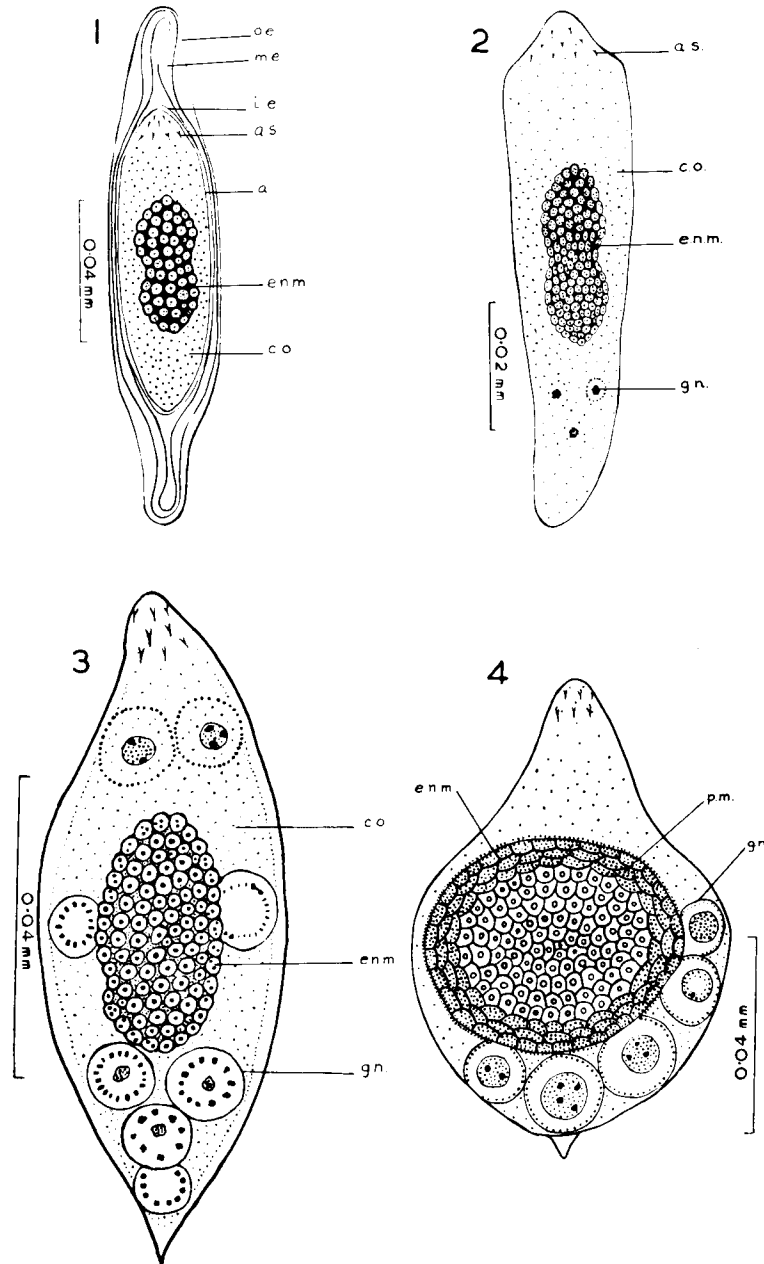
Differing terminologies have been used in the past for subsequent developmental stages. The term 'acanthella' was proposed by Van Cleave (1937) for all stages between the acanthor and the infective juvenile, or cystacanth. This name has been nearly universally accepted and is used here.

8.2.2 *Acanthella*

Upon hatching, the spindle-shaped acanthor immediately increases in size and begins cutting actions with its acic organ. After penetrating into the wall of the mesenteron of the intermediate host it may cease activities for hours or even days, or it may proceed through the wall of

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Fig. 8.2. Development of *Echinorhynchus truttae*. 1, Mature egg. 2, Acanthor removed from the hemocoel of *Gammarus pulex* 11.5 h after infection. 3, Twelve-day embryo. 4, Eighteen-day acanthella. 5, Twenty four-day acanthella. 6, Thirty two-day acanthella. 7, Thirty



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seven-day acanthella. 8, Posterior half of male acanthella, 39 days after infection. a, acanthor; a.s., spine of acanthor; a.t., anterior testis; b.m., muscle layer of body wall; c, cuticula; c.g., cement gland; c.o., cortex; e.n.m., embryonic nuclear mass; g., ganglion; g.n., cortical giant nucleus; i.e., inner envelope of egg; m.e., middle shell of egg; n.r., nucleus of proboscis retractors; o.e., outer envelope of egg; p.b., primordium of copulatory bursa; p.c., primordium of cement gland; p.g., primordium of genitalia; p.g.g., primordium of gonad and genitalia; p.m., primordium of muscles of body wall; p.p., primordium of definitive proboscis; p.p.a., primordium of proboscis apparatus; p.p.r., primordium of proboscis retractors; p.s., proboscis sheath; r.a., remains of acanthor; s., Saeftigen's pouch; s.c., subcuticula; s.d., primordium of sperm duct; s.f., space filled with orange fluid; s.r., retractor muscle of proboscis sheath; t., testis. (From Awachie, 1966.)

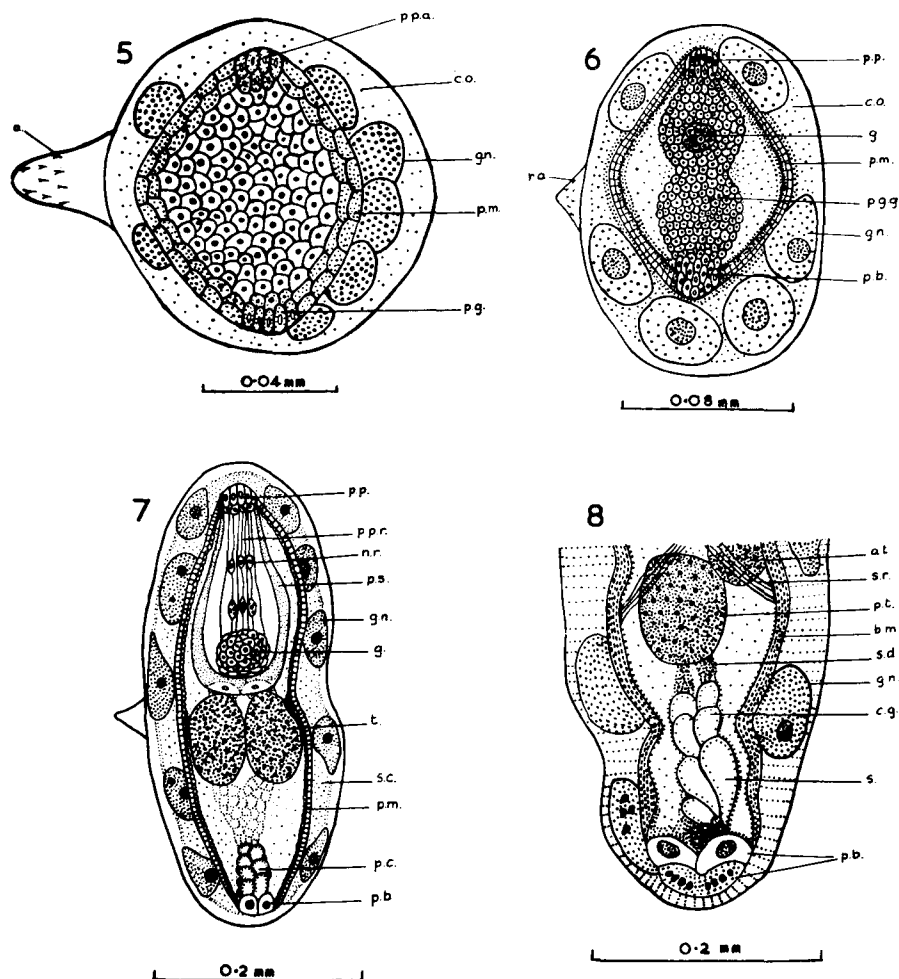
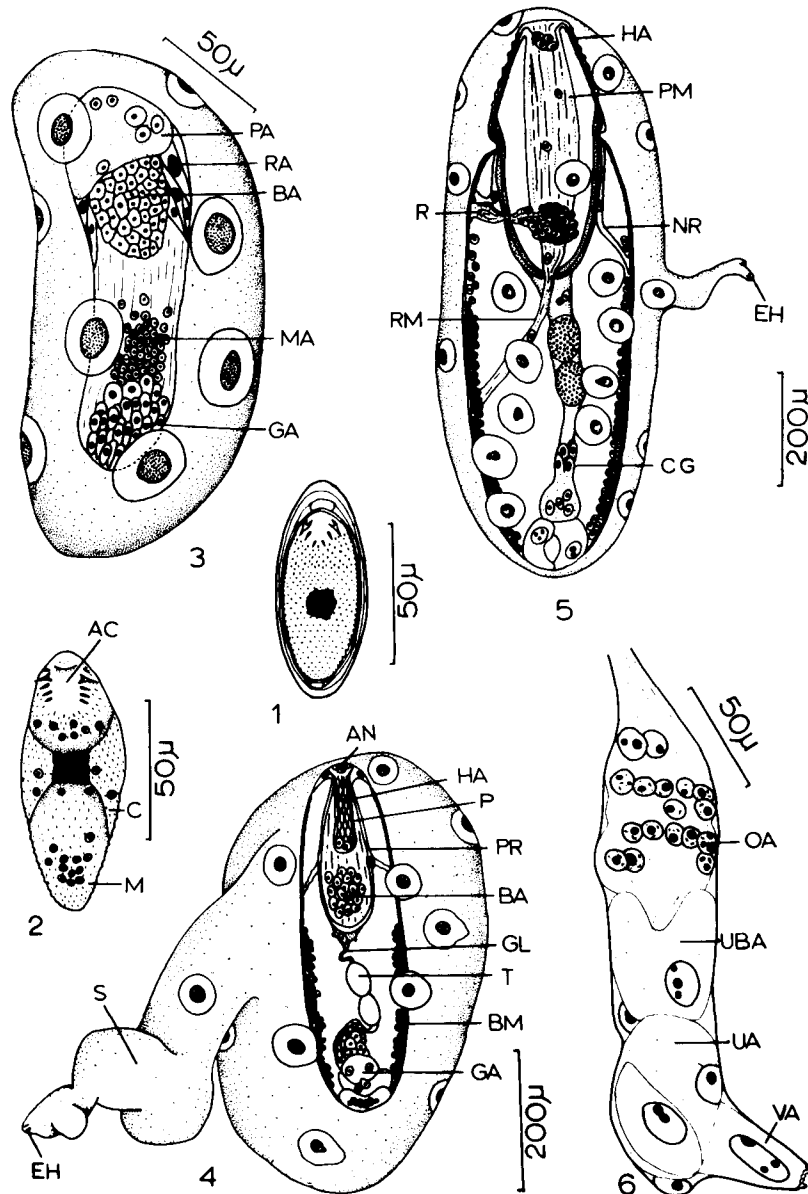


Fig. 8.3. Development of *Plagiorhynchus cylindraceus*. 1, Egg, containing mature acanthor. 2, Acanthor after escape from egg. 3, Acanthella, 22 days. 4, Acanthella, 25 days. 5, Acanthella, 27 days. 6, Anlagen of female reproductive system, 32 days. 7, Developing brain with principal nerve trunks, 28 days. 8, Cross-section at level of developing proboscis, 25 days. 9, Acanthella, 30 days. 10, Cystacanth, 37 days. 11, Cystacanth, 60 days, proboscis artificially forced to evert. AC, acolid organ; AN, apical nuclei; B, bursa; BA, brain anlage; BM, anlagen of body wall musculature; C, cortex; CG, cement glands; EH,



the intestine. In most cases, if not all, the entire acanthor stops under the serosa and begins to grow. Growth first appears as a swelling outward, toward the hemocoel of the host, in a direction 90 degrees from the longitudinal axis of the acanthor. The cortical nuclei enlarge and become vesicular (Fig. 8.2). Their number may increase or not, depending on the species. As growth proceeds, the central nuclear mass begins to organize itself into distinct regions which are the primordia of the internal structures of the adult worm (Fig. 8.2). The proboscis apparatus primordium is a syncytium containing a number of nuclei (Fig. 8.3). Immediately posterior to it, a large mass of nuclei forms the primordium of the brain, while the rest of the nuclear mass elongates behind it. This nuclear mass will become the muscular and reproductive elements of the body. Some nuclei continue to divide while others cease, establishing the eutelic number for a given structure.

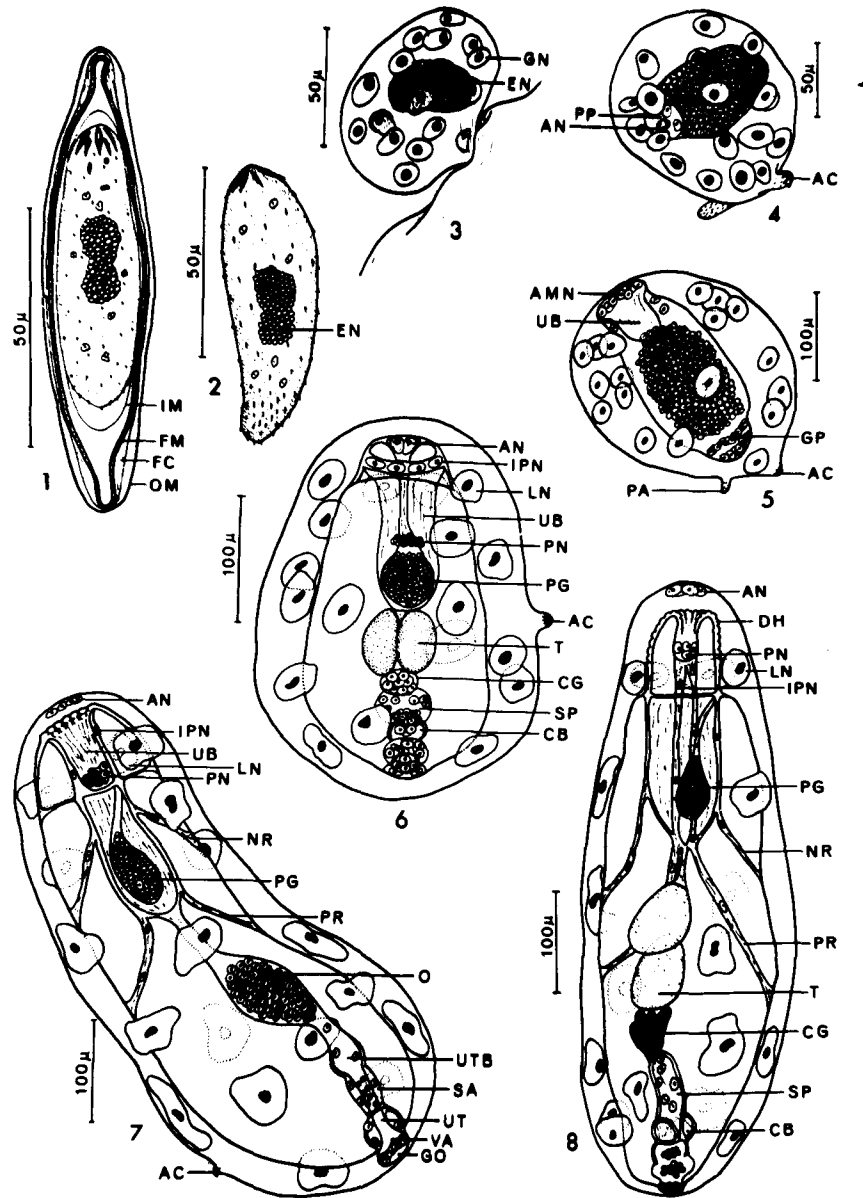
About this time a split occurs between the cortical and medullary regions (Fig. 8.3). Many nuclei migrate to the cortical side of the pseudocoel to begin forming the circular and longitudinal muscle layers of the body wall. Others form a longitudinal strand in the middle of the body cavity; this will differentiate into the genital ligament and associated organs. Shortly after, the sex of the worm can be ascertained.

The nuclei of the proboscis apparatus primordium rearrange themselves. A few migrate to its extreme apex, to become the apical nuclei (Fig. 8.4). Others form the proboscis apical ring at its posterior end. Posterior to these nuclei is the large primordium of the brain, which, along with the proboscis primordium, becomes encased within the proboscis receptacle. The syncytium between the apical nuclei and the proboscis nuclear ring begins to

Fig. 8.4. Development of *Echinorhynchus lageniformis*. 1, Egg. 2, Acanthor removed from amphipod serosa 2 days after infection. 3, Young acanthella attached to host serosa 5 days postinfection. 4, Ten-day acanthella. 5, Thirteen-day acanthella. 6, Fifteen-day male acanthella. 7, Eighteen-day female acanthella. 8, Male acanthella 20 days postinfection. AC, acanthor; AMN, apical and proboscis inveter nuclei mixed; AN, apical nuclei; CB, copulatory bursa; CG, cement glands; DH, developing hooks; EN, entoblast; FC, fibrillar coat; FM, fertilization membrane; GN, giant nuclei; GO, genital opening; GP, nuclei of genital primordium; IM, inner membrane; IPN, proboscis inveter nuclei; LN, lemniscal giant nuclei; NR, neck retractor; O, ovary; OM, outer membrane; PA, posterior end of acanthor; PG, proboscis ganglion; PN, posterior proboscis nuclei or proboscis nuclear ring; PR, proboscis retractor; PP, proboscis primordium; SA, selector apparatus; SP, Saeftigen's pouch; T, testis; UB, uncino-genous bands; UT, uterus; UTB, uterine bell; VA, vagina. (From Olson & Pratt, 1971.)

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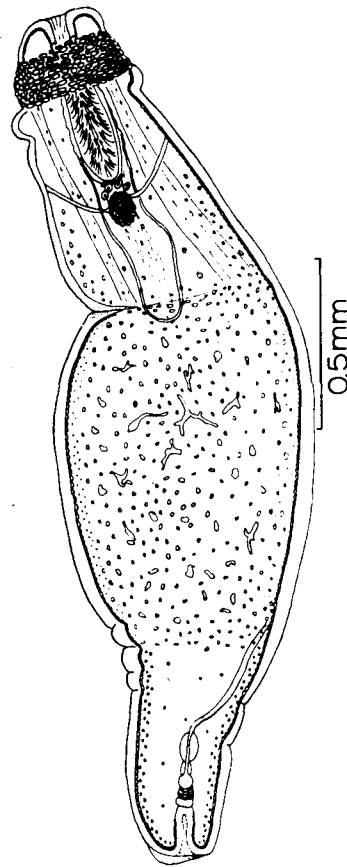
differentiate into uncinogenous bands. These are strandlike, longitudinal thickenings, which alternately swell and constrict. Each swelling will eventually produce a proboscis hook.

The proboscis nuclear ring begins to migrate anteriad, while at the same time the uncinogenous bands arch posteriad, in effect turning themselves inside out. Their outer surfaces bear the swellings that will form the hooks. Strands of tissue remain attached to the nuclei and extend from them back to the base of the receptacle. These will form the retractor muscles.

By this time a few cortical nuclei have formed a ring at the level of the base of the proboscis. Known as the lemniscal ring these nuclei will later migrate into the developing lemnisci.

The brain ganglion extends processes laterad and anteriad to continue

Fig. 8.5. Late acanthella (natural infection in *Macrobrachium* sp.), showing ameoboid and fragmenting nuclei of the body wall. (From Schmidt & Kuntz, 1967*a*.)



the development of the nervous system. Gonads increase in size within the genital ligament, and associated genital organs are rapidly differentiating near the posterior end.

As internal organs continue growing, the cortical layer gets thinner. In several species a stalk, bearing the hooks of the acolid organ, has been described, extending from the side of the embryo (Figs 8.2, 8.3, 8.4). They eventually disappear, but demonstrate two important phenomena: the axis of the adult worm is rotated 90 degrees from that of the acanthor, and the outer tegument of the acanthella is the stretched tegument of the acanthor.

If the adult of the species has giant nuclei in the body wall, these nuclei continue to enlarge and migrate to their definitive locations at this time. If the adult has nuclear fragments in its body wall, the cortical nuclei become ameboid (Fig. 8.5), with long processes that break up and move to their proper locations.

After the proboscis anlagen has everted, hook development proceeds rapidly, soon piercing the tegument and growing to the final size found in the adult worm. Morphogenesis and an analysis of hook structure of *Moniliformis* was presented by Hutton & Oetinger (1980).

By this time the lemnisci have begun their inward growth, with the nuclei of the lemniscal ring following them in. This growth process must be very rapid, for few researchers have reported seeing it.

Neck retractor muscles, proboscis retractor and protruder muscles, nervous system, and all other organs are now essentially complete and in place. The proboscis then invaginates, at least in most species. In some species the neck retractor muscles pull the entire praesoma into the body, while the posterior end is also pulled in. This is particularly true of parasites of birds, where they must be able to withstand the grinding action of the host's ventriculus.

8.2.3 *Cystacanth*

The worm now has all of the structures of the adult and is capable of infecting the definitive host. Essentially a juvenile, it is most commonly called a cystacanth. Cable & Dill (1967) made a point for calling this stage a juvenile rather than a cystacanth, because it is unencysted and differs from the adult only in size and degree of sexual development. The name cystacanth would be more appropriate to juveniles encysted in the tissues of a paratenic host, according to those authors. Even so, I prefer to follow common usage in this case and use this name for the stage that has completed development in the intermediate host and is infective to the definitive host. In most, if not all, species the cystacanth in the intermediate host is surrounded by a thin membranous envelope. Whether this membrane

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is of host or parasite origin has received considerable attention. The literature was reviewed by Wanson & Nickol (1973), who concluded that the envelope is in fact the stretched body covering of the acanthor. It is quite possible that in some cases this layer is thickened by a contribution from the host's defensive cells. Factors that influence the activation of cystacanths were reviewed by Graff & Kitzman (1965).

Paratenic hosts often are important ecological bridges between the intermediate and definitive hosts, such as the ostracod–bluegill sunfish–black bass cycle of *Neoechinorhynchus cylindratus*, as outlined by Ward (1940a) (see below). But because no further development occurs in the paratenic host, this stage is not considered further here, except to note that a possible exception is seen in the case of *Sphaerechinorhynchus serpenticola*. Worms of this species have been found in the intestinal mesenteries of several species of snakes and without exception the individuals were nearly adults, with active sperm formation in the males. Inseminated females have not been found.

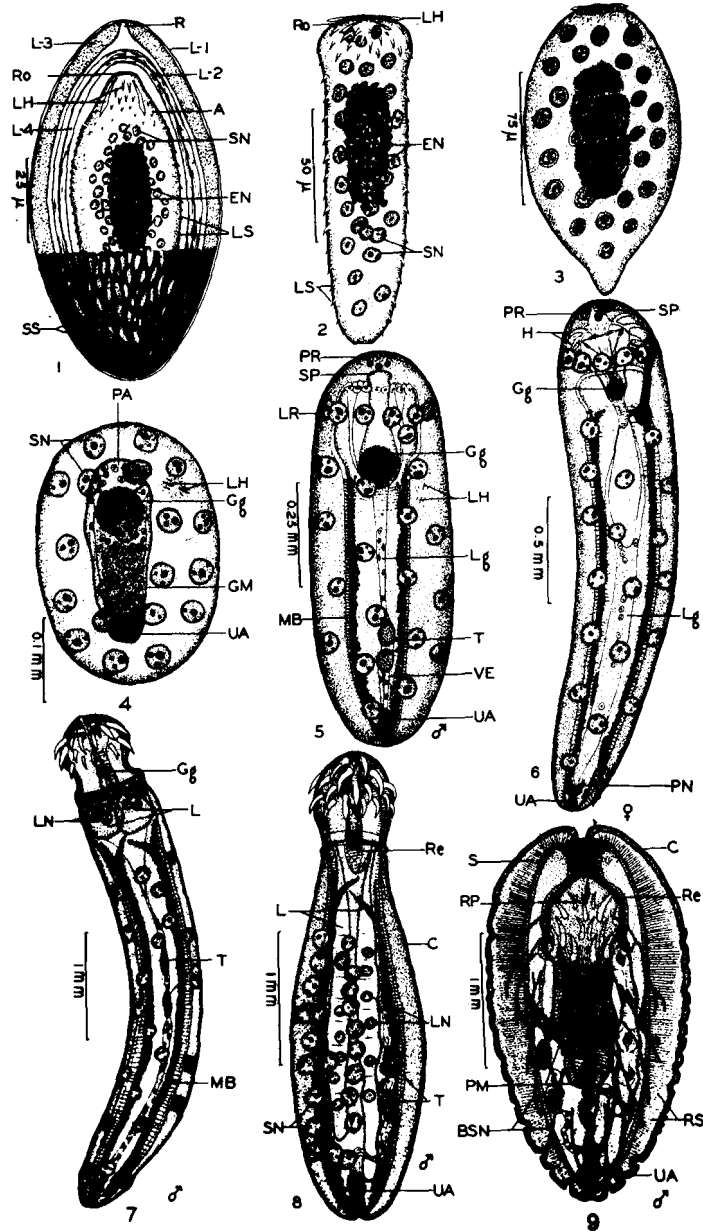
8.3 Life cycles

Too many life cycles are known for all of them to be reviewed here. Table 8.1 lists records of known intermediate and paratenic hosts, with references, that have accumulated since Meyer's (1933) list. An illustrative sampling of life cycles within the three classes of Acanthocephala are listed below.

8.3.1 Class Archiacanthocephala

Moore (1946b) produced laboratory infections of *Macracanthorhynchus ingens* in the scarabaeid beetles *Phyllophaga crinita*, *P. hirtiventris* and *Ligyrus* sp. Crites (1964) found a natural infection of this species in

Fig. 8.6. Development of *Macracanthorhynchus hirudinaceus*. 1, Egg. 2, Acanthor. 3, Very early acanthella. 4, Early acanthella. 5, Acanthella. 6, Late acanthella. 7, Early cystacanth. 8, Cystacanth before invagination. 9, Invaginated cystacanth. A, infective acanthor; BSN, branched skin nuclei; C, cuticle; EN, embryonic nuclear mass (condensed nuclei); GM, gonad and muscle primordia; Gg, ganglion; H, hooks; L, lemnisci; L-1, L-2, L-3, L-4, four shell layers; Lg, ligament; LH, larval hooks; LN, lemnis nuclei; LR, lemniscus nuclear ring; LS, larval spines; MB, muscle cell band; PA, proboscis primordium; PM, proboscis musculature; PN, protonephridia; PR, proboscis nuclear ring; R, raphe; Re, receptaculum; RO, rostellum; RP, retracted proboscis; RS, radial skin fibers; S, skin; SS, scalloped shell; SN, skin or subcuticular nuclei; SP, sensory papilla; T, testes; UA, urogenital primordium (except gonads); VE, vasa efferentia. (After Kates, 1943.)



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a millipede, and Elkins & Nickol (1983) found *M. ingens* cystacanths in woodroaches (*Parcoblatta pennsylvanica*). Definitive hosts are racoons and black bears.

Kates (1943) repeated earlier studies on the development of *M. hirudinaceus* in dung beetles (Fig. 8.6).

Moore (1962) traced the development of *Mediorhynchus grandis* in grasshoppers (*Chortophaga viridifasciata*, *Orphulella pelidna*, *Arphia luteola* and *Schistocerca americana*). Cystacanths were infective to birds in 27–30 days.

Nickol (1977) reported the development of *Mediorhynchus centurorum* in woodroaches, *Parcoblatta pennsylvanica*. Cystacanths were infective to woodpeckers in about 47 days.

8.3.2 *Class Palaeacanthocephala*

Awachie (1966) found *Echinorhynchus truttae* to develop in *Gammarus pulex* (Fig. 8.2). Cystacanths were infective to trout, *Salmo trutta*, in about 82 days.

Amin (1982) described the development of *Acanthocephalus dirus* in the isopod *Caecidotea militaris*. Its definitive hosts are fishes.

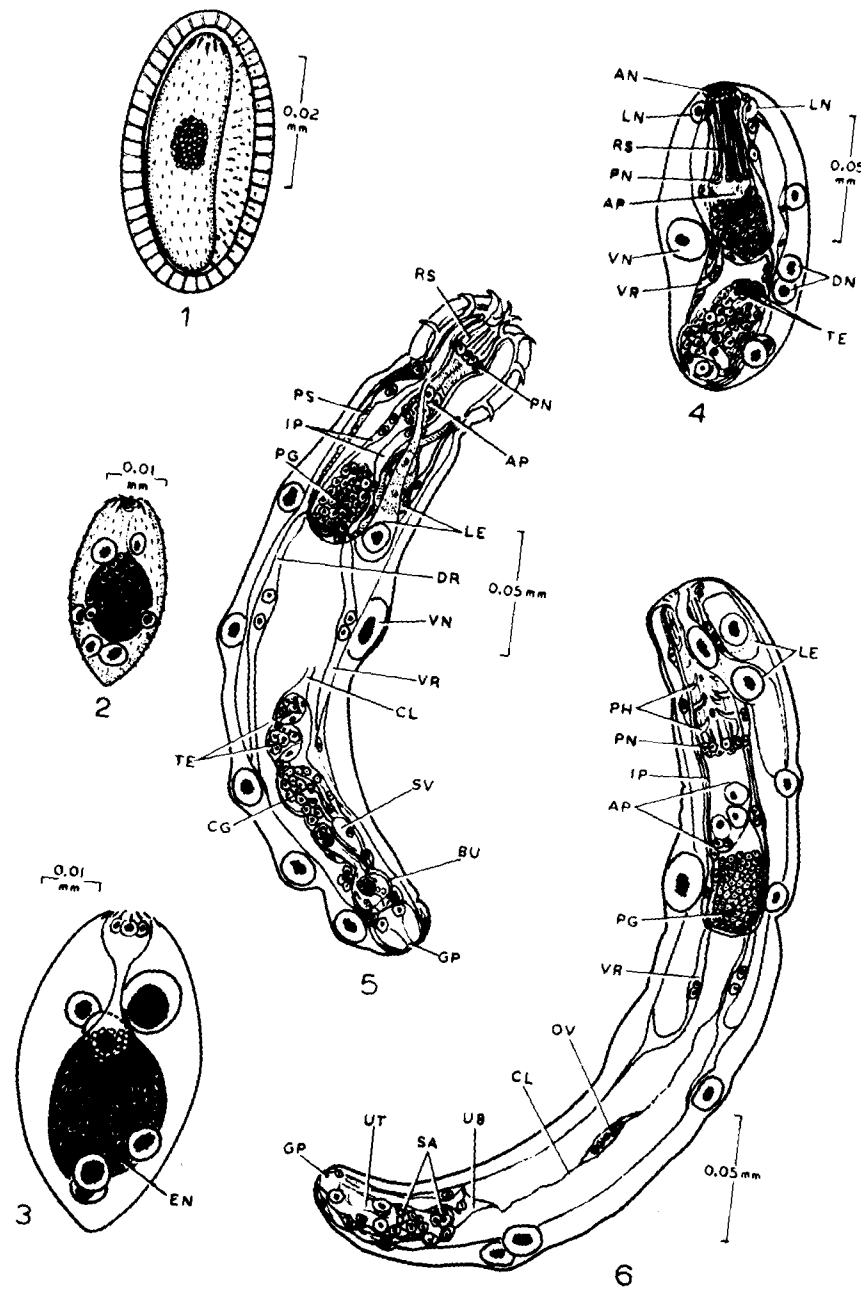
Olson & Pratt (1971) demonstrated the development of *Echinorhynchus lageniformis* in the amphipod *Corophium spinicorne* (Fig. 8.4). The cystacanth becomes infective to starry flounders, *Platichthys stellates*, in about 30 days.

Hynes & Nicholas (1957) reported the development of *Polymorphus minutus* in the amphipod *Gammarus pulex*. A wide variety of ducks serve as definitive hosts.

Fig. 8.7. Development of *Paulisentis fractus*. 1, Egg or shelled embryo drawn from living specimen. 2, Acanthor from hemocoel of copepod one hour after exposure to infection. 3, Three-day acanthor. 4, Young acanthella from copepod 7 days after exposure to infection. One nucleus of future lemnisci omitted for clarity. 5, Late acanthella (male) with proboscis everted; from copepod 9 days after exposure. 6, Late acanthella (female) with proboscis inverted; from copepod 9 days after exposure. AN, apical nuclei; AP, apical organ primordium; BU, bursa; CG, cement gland; CL, central ligament; DN, dorsal giant nuclei of trunk wall; DR, dorsal retractor of proboscis receptacle; EN, embryonal nuclear mass; GP, genital pore; IP, inverter of proboscis; LE, lemniscus; LN, nucleus of lemnisci; OV, ovary; PG, proboscis ganglion; PH, proboscis hooks; PN, proboscis nuclear ring; PS, muscular sheath of proboscis receptacle; RS, uncinogenous bands; SA, selector apparatus; SV, seminal vesicle; TE, testes; UB, uterine bell; UT, uterus; VN, ventral giant nucleus of trunk wall; VR, ventral retractor of proboscis receptacle. (From Cable & Dill, 1967.)

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Schmidt & Olson (1964) traced the development of *Plagiorhynchus cylindraceus* in the terrestrial isopods *Armadillidium vulgare*, *Porcellio laevis* and *P. scaber* (Fig. 8.3). The cystacanth becomes infective to birds in 60–65 days.

8.3.3 *Class Eoacanthocephala*

Cable & Dill (1967) found *Paulisentis fractus* to develop in the copepod *Tropocyclops prasinus*. Cystacanths were infective to creek chubs, *Semotilus atromaculatus*, in 13 days after hatching (Fig. 8.7).

Ward (1940*a*) described the development of *Neoechinorhynchus cylindratus* in the ostracod *Cypria* (*Physacypria*) *globula*. She emphasized the important role of the bluegill sunfish, *Lepomis macrochirus*, as a paratenic host between the crustacean and the black bass, *Micropterus salmoides*, definitive host.

Uglen & Larson (1969) demonstrated the development of *Neoechinorhynchus saginatus* in the ostracod *Cypridopsis vidua*. The cystacanths were infective to creek chubs on the sixteenth day. Paratenic hosts were not discovered.

Harms (1965*a*) reported the development of *Octospinifer macilentus* in the ostracod *Cyclocypris serena*. Cystacanths were infective to white suckers, *Catostomus commersoni*, in about 30 days.

Table 8.1. *Intermediate and paratenic hosts for Acanthocephala, with references that have accumulated since Meyer's list of 1933*

Species	Intermediate host	Paratenic host	Reference
CLASS ARCHIACANTHOCEPHALA			
ORDER GIGANTORHYNCHIDA			
Family Gigantorhynchidae			
<i>Mediorhynchus centurorum</i>	<i>Parcoblatta pensylvanica</i>		Nickol (1977)
<i>Mediorhynchus grandis</i>	<i>Arphia luetola</i>		Moore (1962)
	<i>Chortophaga viridifasciata australior</i>		Moore (1962)
	<i>Gryllus</i> sp.		Moore (1962)
	<i>Orphulella pelidna</i>		Moore (1962)
	<i>Schistocerca americana</i>		Moore (1962)
<i>Mediorhynchus micracanthus</i>	<i>Adesmia gebleri</i>	<i>Blarina brevicauda</i>	Collins (1971)
<i>Mediorhynchus papillosus</i>	Coleoptera		Rizhikov & Dizer (1954)
	<i>Pimelia subglobosa</i>		Kabilov (1969)
	<i>Stalagmoptera staundingeri</i>		Ivashkin & Shmitova (1969)
	<i>Tenthyria taurica</i>		Gafurov (1975)
<i>Mediorhynchus</i> sp.	<i>Zophosis punctata</i>		Ivashkin & Shmitova (1969)
Gigantorhynchidae	<i>Gammarus lacustris</i>		Gafurov (1975)
	<i>Gammarus lacustris</i>		Borgarenko (1975)
<i>Gigantorhynchus</i> sp.	<i>Orchestoidea trinitatis</i>		Borgarenko, Bronshpits & Solodenko (1975)
			Tsimbalyuk, Kulikov, Ardasheva & Tsimbalyuk (1978)
ORDER MONILIFORMIDA			
Family Moniliformidae			
<i>Moniliformis clarki</i>	<i>Ceuthophilus fusiformis</i>		Buckner & Nickol (1975)
	<i>Ceuthophilus utahensis</i>		Crook (1964); Crook & Grundmann (1964)
	<i>Eleodes tuberculata patralis</i> – incomplete development		Crook (1964)
<i>Moniliformis merionis</i>	<i>Blaps</i> sp.		Golvan & Theodorides (1960)
<i>Moniliformis moniliformis</i>	<i>Blaps deplanata reichardti</i>		Gafurov (1970)
	<i>Blaps holofila</i>		Ivashkin (1956)
	<i>Blatella germanica</i>		Gonzalez & Mishra (1976)
	<i>Geotrupes impressus</i>		Sultanov, Kabilov & Davlatov (1974)
	<i>Periplaneta americana</i>		Yamaguti & Miyata (1942); Sita (1949); Coronel Guevara, (1953); Bonfonte, Faust & Giraldo

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Table 8.1. (cont.)

Species	Intermediate host	Paratenic host	Reference
<i>Moniliformis moniliformis</i>	<i>Periplaneta americana</i>		(1961); Moore (1962); King & Robinson (1967); Mercer & Nicholas (1967); Robinson & Strickland (1969); Lackie (1972 <i>a, b</i>); Rotheram & Crompton (1972); Acholonu & Finn (1974); Brennan & Cheng (1975); Anvar & Paran (1976); Hutton & Oettinger (1980)
	<i>Prosodes biformis</i>		Gafurov (1970)
	<i>Prosodes vincens</i>		Gafurov (1970)
	<i>Scarabaeus sacer</i>		Nazarova (1959)
<i>Moniliformis</i> sp.	<i>Periplaneta americana</i>		Bhamburkar, Garde & Shastri (1970)
ORDER OLIGACANTHORHYNCHIDA			
Family Oligacanthorhynchidae			
<i>Macracanthorhynchus catulinus</i>	<i>Adesmia gebleri</i>		Rizhikov & Dizer (1954); Gafurov (1970)
	<i>Dissonomus</i> sp.		Gafurov (1970)
	<i>Pachyscelis banghaasi</i>		Gafurov (1970)
	<i>Stalagmoptera incostata</i>		Gafurov (1970)
	<i>Tentyria tessulata</i>		Farzaliev & Petrochenko (1980)
	<i>Trigonoscelis gemmulata</i>		Gafurov (1970)
		<i>Agama caucasica</i>	Gafurov (1970)
		<i>Coluber jugularis</i>	Gafurov (1970)
		<i>Citellus dauricus</i>	Dubin (1948)
		<i>Eremias pleskei</i>	Farzaliev & Petrochenko (1980)
		<i>Erinaceus dauricus</i>	Dubin (1948)
		<i>Eumeces schneideri</i>	Farzaliev & Petrochenko (1980)
		<i>Lacerta strigata</i>	Farzaliev & Petrochenko (1980)
		<i>Marmota siberica</i>	Dubin (1948)
		<i>Meles meles raddei</i>	Dubin (1948)
		<i>Mustela nivalis</i>	Dubin (1948)
		<i>Naja oxiana</i>	Markov, Bogdanov, Makeev & Khutoryanski (1968)
		<i>Ophisaurus apodus</i>	Farzaliev & Petrochenko (1980)
		<i>Putorius eversmanni</i>	Dubin (1948)
		<i>Rana ridibunda</i>	Farzaliev & Petrochenko (1980)

Table 8.1. (cont.)

Species	Intermediate host	Paratenic host	Reference
<i>Macracanthorhynchus catulinus</i>		<i>Uromastix hardwicki</i> <i>Varanus benghalensis</i> <i>Vipera lebetina</i>	Barus & Tenora (1976) Barus & Tenora (1976) Markov, Zinyakova & Lutta (1967)
<i>Macracanthorhynchus hirudinaceus</i>	<i>Anomala mongolica</i> <i>Aphodius subterraneus</i> <i>Bricoptis variolosa</i> <i>Catonia aurata</i> <i>Copris lunaris</i> <i>Cotinus nitida</i> <i>Cryotes nasicornis</i> <i>Dorcadion pedestrae</i> <i>Dorystenes hydropicus</i> <i>Dorystenes paradoxus</i> <i>Geotrupes stercorarius</i> <i>Geotrupes</i> sp. <i>Gnaptor spinimanus</i> <i>Gymnopleurus mopsus</i> <i>Harpatus tridens</i> <i>Heteoligus</i> sp. <i>Holotrichia titanus</i> <i>Liocola brevitarsis</i> <i>Melolontha hippocastani</i> <i>Melolontha melolontha</i> <i>Mimela splendens</i> <i>Oryctes nasicornis</i> <i>Periplaneta americana</i> <i>Phyllodromia germanica</i> <i>Phyllophaga anxia</i> <i>Phyllophaga futilis</i> <i>Phyllophaga rugosa</i> <i>Poecilos</i> sp. <i>Polyphylla laticolis</i> <i>Polyphylla olivieri</i> <i>Popillia japonica</i> <i>Popillia</i> sp. <i>Rhizotrogus aestivus</i>	<i>Vulpes korsak</i>	Dubinin (1948) Leng, Huang & Liang (1981) Chebotarev (1954) Daynes (1966) Shcherbovich (1950) Trifonov (1963); Sadaterashvili (1970) Kates (1943) Chebotarev (1954) Trifonov (1961) Leng, Huang & Liang (1981) Leng, Huang & Liang (1981); Wang, Li & Cai (1981) Sadaterashvili (1970); Kashnikov (1972) Chebotarev (1954); Morozov (1959) Trifonov (1961) Ono (1933) Ono (1933) Simmonds (1960) Leng, Huang & Liang (1981) Oparin (1962) Shcherbovich (1950) Shcherbovich (1950) Leng, Huang & Liang (1981) Sadaterashvili (1970); Kashnikov (1972) Robinson & Strickland (1969) Ono (1933) Swales & Gwatkin (1948) Swales & Gwatkin (1948) Swales & Gwatkin (1948) Trifonov (1961) Leng, Huang & Liang (1981) Sadaterashvili (1970) Miller (1943) Leng, Huang & Liang (1981) Sadaterashvili (1970)

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Table 8.1. (cont.)

Species	Intermediate host	Paratenic host	Reference
<i>Macracanthorhynchus ingens</i>	<i>Floridobolus penneri</i>		Bowen (1967)
	<i>Ligyris</i> sp.		Moore (1946 <i>b</i>)
	<i>Narceus americanus</i>		Crites (1964)
	<i>Narceus gordanus</i>		Bowen (1967)
	<i>Parcoblatta pennsylvanica</i>		Elkins & Nickol (1983)
	<i>Phyllophaga crinita</i>		Moore (1946 <i>b</i>)
	<i>Phyllophaga hirtiventris</i>		Moore (1946 <i>b</i>)
		<i>Agkistrodon piscivorus</i>	Elkins & Nickol (1983)
		<i>Coluber constrictor</i>	Elkins & Nickol (1983)
		<i>Dasybus novemcinctus</i>	Elkins & Nickol (1983)
		<i>Elaphe obsoleta</i>	Elkins & Nickol (1983)
		<i>Lampropeltis getulus</i>	Elkins & Nickol (1983)
		<i>Nerodia cyclopion</i>	Elkins & Nickol (1983)
		<i>Nerodia fasciata</i>	Elkins & Nickol (1983)
<i>Macracanthorhynchus</i> larvae	<i>Amphimallon solstitialis</i>		Moore (1946 <i>b</i>)
	<i>Amphimallon solstitialis setosus</i>		Elkins & Nickol (1983)
	<i>Anoxia pilosa</i>		Moore (1946 <i>b</i>)
	<i>Rhyzotrogus aestivus</i>		Elkins & Nickol (1983)
		<i>Thamnophis sirtalis</i>	Sadaterashvili (1978 <i>a</i>)
<i>Oncicola canis</i>		<i>Dasybus novemcinctus texanus</i>	Sadaterashvili (1978 <i>b</i>)
<i>Oncicola onicola</i>		<i>Gallus gallus domesticus</i>	Chandler (1946 <i>a</i>)
		<i>Leptoptila verreauxi ochroptera</i>	Zeledón & Arroyo (1960)
		<i>Aphelocephala leucopsus</i>	Pereira (1936)
<i>Oncicola pomatostomi</i>		<i>Climacteris leucophaea</i>	Schmidt (1983)
		<i>Climacteris picumnus</i>	Schmidt (1983)
		<i>Climacteris wellsi</i>	Schmidt (1983)
		<i>Cynclosoma castaneum</i>	Schmidt (1983)
		<i>Cynclosoma cinnamomeum</i>	Schmidt (1983)
		<i>Cynclosoma rufiventris</i>	Schmidt (1983)
		<i>Excalfactoria lineata</i>	Schmidt (1983)
		<i>Hylacola pyrrhopgyia</i>	Schmidt (1983)
		<i>Hypotaenidia philippensis</i>	Schmidt (1983)
		<i>Oreocicha lunulata</i>	Schmidt (1983)
		<i>Pachycephala inornata</i>	Schmidt (1983)
		<i>Pedionomus torquatus</i>	Schmidt (1983)
		<i>Pomatostomus rubeculus</i>	Schmidt (1983)
		<i>Pomatostomus ruficeps</i>	Schmidt (1983)
		<i>Pomatostomus superciliosus</i>	Schmidt (1983)
		<i>Pomatostomus temporalis</i>	Schmidt (1983)
		<i>Pyrrholaemus brunnus</i>	Schmidt (1983)
		<i>Seriocornis maculatus</i>	Schmidt (1983)

Table 8.1. (cont.)

Species	Intermediate host	Paratenic host	Reference
<i>Oncicola schacheri</i>		<i>Meles meles</i>	Schmidt (1972c)
<i>Oncicola spirula</i>	<i>Blabera fusca</i>		Brumpt & Desportes (1938)
	<i>Blatella germanica</i>		Brumpt & Urbain (1938); Dollfus (1938); Van Thiel & Wiegand-Bruss (1945); Eckert (1961)
	<i>Periplaneta orientalis</i>		Brumpt & Urbain (1938)
	<i>Rhyparobia maderae</i>		Brumpt & Desportes (1938)
<i>Oncicola</i> sp.		<i>Coturnix coturnix</i>	Padmavathi (1967)
		<i>Francolinus pondicerianus</i>	Padmavathi (1967)
<i>Prosthenorchis elegans</i>	<i>Blabera fusca</i>		Brumpt & Desportes (1938)
	<i>Blatella germanica</i>		Brumpt & Urbain (1938); Dollfus (1938); Eckert (1961); Wanson & Nickol (1975)
	<i>Lasioderma serricorne</i>		Stunkard (1965)
	<i>Rhyparobia maderae</i>		Brumpt & Desportes (1938)
	<i>Stegobium paniceum</i>		Stunkard (1965)
CLASS PALAEACANTHOCEPHALA			
ORDER ECHINORHYNCHIDA			
Family Cavisomidae			
<i>Neorhadinorhynchus atlanticus</i>	<i>Stenoteuthis pteropus</i>		Naidemova & Zuev (1978); Gaevskaya & Nigmatullin (1981)
Family Echinorhynchidae			
<i>Acanthocephalus anguillae</i>	<i>Asellus aquaticus</i>		Shtein (1959); Andryuk (1974); Andryuk (1979 a, c)
<i>Acanthocephalus anthuris</i>	<i>Proasellus coxalis</i>		Batchvarov (1974)
<i>Acanthocephalus clavula</i>	<i>Asellus meridianus</i>		Chubb (1964); Rojanapaibul (1976)
	<i>Chaetogammarus ischnus</i>		Kurandina (1975)
	<i>Dikerogammarus haemobaphes</i>		Komarova (1969); Kurandina (1975)
	<i>Gammarus balcanicus</i>		Ivashkin (1972)
	<i>Gammarus (Rivulogammarus) balcanicus</i>		Yalynskaya (1980)
	<i>Gammarus (Rivulogammarus) kischeneffensis</i>		Yalynskaya (1980)
	<i>Pallasea quadrispinosa</i>		Shtein (1959)
	<i>Pontogammarus obesus</i>		Kurandina (1975)

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Table 8.1. (cont.)

Species	Intermediate host	Paratenic host	Reference
<i>Acanthocephalus dirus</i>	<i>Asellus intermedius</i>		Seidenberg (1973); Oettinger & Nickol (1981)
	<i>Asellus</i> sp.		Bullock (1962); Camp & Huizinga (1980)
	<i>Caecidotea communis</i>		Muzzall (1981)
	<i>Caecidotea militaris</i>		Amin (1980, 1982); Amin, Burns & Redlin (1980)
	<i>Lirceus garmani</i>		Oettinger & Nickol (1981)
	<i>Lirceus lineatus</i>		Muzzall & Rabalais (1975 <i>a, b, c</i>); Oettinger & Nickol (1981)
	<i>Pontoporeia affinis</i>		Amin (1978 <i>b</i>)
<i>Acanthocephalus galaxii</i>	<i>Paracalliope fluviatilis</i>		Hine (1977)
<i>Acanthocephalus lucii</i>	<i>Asellus aquaticus</i>		Shtein (1959); Andryuk (1979 <i>b, c</i>); Bratney (1980)
	<i>Asellus</i> sp.		Copland (1956)
<i>Acanthocephalus minor</i>	<i>Asellus hilgendorfi</i>		Nagasawa, Egusa & Ishino (1982)
<i>Acanthocephalus ranae</i>	<i>Asellus aquaticus</i>		Kirbanov (1978 <i>a</i>)
<i>Acanthocephalus larvae</i>	<i>Asellus aquaticus</i>		Andryuk (1976)
<i>Echinorhynchus gadi</i>	<i>Caprella septentrionalis</i>		Val'ter (1976); Val'ter, Kondrashkova & Popova (1980)
	<i>Gammarus duebeni</i>		Kulachkova & Timofeeva (1977)
<i>Echinorhynchus lageniformis</i>	<i>Corophium spinicorne</i>		Olson (1970); Olson & Pratt (1971)
<i>Echinorhynchus leidy</i>	<i>Mysis relicta</i>		Prychitko & Nero (1983)
<i>Echinorhynchus salmonis</i>	<i>Hyaella azteca</i>		DeGiusti (1949 <i>b</i>)
	<i>Pontoporeia affinis</i>		Shtein (1959); Brownell (1970)
<i>Echinorhynchus truttae</i>	<i>Gammarus balcanicus</i>		Ivashkin (1972)
	<i>Gammarus</i> (<i>Rivulogammarus</i>) <i>balcanicus</i>		Yalynskaya (1980)
	<i>Gammarus fossarum</i>		Van Maren (1979 <i>a</i>)
	<i>Gammarus</i> (<i>Rivulogammarus</i>) <i>kischeneffensis</i>		Yalynskaya (1980)
	<i>Gammarus pulex</i>		Awachie (1963, 1966, 1967)
	<i>Gammarus pulex fossarum</i>		Schütze & Ankel (1976)
<i>Echinorhynchus</i> sp.	<i>Pontogammarus</i>		Komarova (1969)

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Table 8.1. (*cont.*)

Species	Intermediate host	Paratenic host	Reference
Family Illiosentidae			
<i>Dentitruncus truttae</i>	<i>Echinogammarus roco</i>		Orecchia, Paggi, Manilla & Rossi (1978)
	<i>Echinogammarus tibaldii</i>		Orecchia <i>et al.</i> (1978)
	<i>Gammarus italicus</i>		Orecchia <i>et al.</i> (1978)
<i>Dollfusentis chandleri</i>	<i>Corophium lacustre</i>		Buckner, Overstreet & Heard (1978)
	<i>Grandidierella bonnieroides</i>		Buckner, Overstreet & Heard (1978)
	<i>Lepidactylus</i> sp.		Buckner, Overstreet & Heard (1978)
<i>Tegorhynchus furcatus</i>	<i>Haustorius</i> sp.		Buckner, Overstreet & Heard (1978)
	<i>Lepidactylus</i> sp.		Buckner, Overstreet & Heard (1978)
Family Fessisentidae			
<i>Fessisentis fessus</i>	<i>Asellus forbesi</i>		Buckner (1977); Buckner & Nickol (1979)
	<i>Lirceus lineatus</i>		Buckner (1977); Buckner & Nickol (1979)
<i>Fessisentis necturorum</i>	<i>Asellus scrupulosus</i>		Nickol & Heard (1973)
<i>Fessisentis tichiganensis</i>		<i>Umbra limi</i>	Amin (1980)
Family Pomphorhynchidae			
<i>Pomphorhynchus bulbocolli</i>	<i>Gammarus</i> sp. <i>Hyalella azteca</i>		Muzzall (1981) Schmidt (1964 <i>a</i>); Muzzall (1981)
		<i>Ameiurus nebulosus</i>	Bangham (1955)
		<i>Ictalurus melas</i>	Sutherland & Holloway (1979)
		<i>Notropis hudsonius</i>	Bangham (1955)
		<i>Osmerus mordax</i>	Bangham (1955)
		<i>Perca flavescens</i>	Bangham (1955)
		<i>Percopsis omiscomaycus</i>	Bangham (1955)
		<i>Umbra limi</i>	Bangham (1955)
<i>Pomphorhynchus dubious</i>		<i>Rana cyanophylctis</i>	Kaw (1941)
<i>Pomphorhynchus laevis</i>	<i>Corophium volutator</i> <i>Gammarus bergi</i>		Engelbrecht (1957) Chibichenko & Mamytova (1978)
	<i>Gammarus fossarum</i> <i>Gammarus lacustris</i>		Van Maren (1979 <i>a, b</i>) Chibichenko & Mamytova (1978)
	<i>Gammarus pulex</i>		Marshall (1976); Rumpus & Kennedy (1974)
	<i>Gammarus</i> sp. <i>Pontogammarus robustoides</i>		Engelbrecht (1957) Komarova (1969)

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Table 8.1. (cont.)

Species	Intermediate host	Paratenic host	Reference
<i>Pomphorhynchus perforator</i>	<i>Gammarus bergi</i> <i>Gammarus lacustris</i>		Chibichenko & Mamytova (1978) Chibichenko & Mamytova (1978)
<i>Pomphorhynchus rocci</i>	<i>Gammarus tigrinus</i>		Johnson & Harkema (1971)
Family Rhadinorhynchidae			
<i>Australorhynchus tetramorphacanthus</i>		<i>Paratrigla papilo</i>	Lebedev (1967)
<i>Golvanacanthus problematicus</i>	<i>Gammarus olivii</i>		Mordvinova & Parukhin (1978)
<i>Leptorhynchoides plagicephalus</i>	<i>Gammarus pulex</i>		Rasin (1949)
<i>Leptorhynchoides thecatus</i>	<i>Hyaella azteca</i> <i>Hyaella knickerbockeri</i>		DeGiusti (1949 <i>a</i>); Uznanski & Nickol (1976, 1980 <i>a, b</i>) DeGiusti (1939)
		<i>Ambloplites rupestris</i>	DeGiusti (1949 <i>a</i>)
		<i>Lepomis cyanellus</i>	Samuel, Nickol & Mayes (1976)
		<i>Lepomis gibbosus</i>	Samuel, Nickol & Mayes (1976)
		<i>Micropterus salmoides</i>	Samuel, Nickol & Mayes (1976)
<i>Serrasentis sagittifer</i>		<i>Pagellus erythrinus</i>	Orecchia, Paggi & Hannuna (1970)
ORDER POLYMORPHIDA			
Family Centrorhynchidae			
<i>Centrorhynchus amphibius</i>		<i>Ptyas mucosus</i> <i>Rana tigrina</i>	Das (1950) Das (1950)
<i>Centrorhynchus batrachus</i>		<i>Rana tigrina</i>	Das (1952)
<i>Centrorhynchus crocidurus</i>		<i>Crocidura caerulea</i>	Das (1950)
<i>Centrorhynchus falconis</i>		<i>Ptyas mucosus</i>	Das (1957 <i>a</i>)
<i>Centrorhynchus longicephalus</i>		<i>Lycodon</i> sp.	Das (1950)
<i>Centrorhynchus magnus</i>		<i>Rana tigrina</i>	Schmidt & Kuntz (1969)
<i>Centrorhynchus microcervicanthus</i>		<i>Naia tripudians</i>	Das (1950)
<i>Centrorhynchus mysentri</i>		<i>Rana tigrina</i>	Gupta & Fatma (1983)
<i>Centrorhynchus ptyasus</i>		<i>Ptyas mucosus</i>	Gupta (1950)
<i>Centrorhynchus spilornae</i>		<i>Agkistrodon acutus</i> <i>Dinodon rufozonatum</i> <i>Psammodynastes pulverulentis</i> <i>Trimeresurus mucrosquamatus</i> <i>Trimeresurus stejnegeri</i>	Schmidt & Kuntz (1969) Schmidt & Kuntz (1969) Schmidt & Kuntz (1969) Schmidt & Kuntz (1969) Schmidt & Kuntz (1969)

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Table 8.1. (*cont.*)

Species	Intermediate host	Paratenic host	Reference
<i>Centrorhynchus spinosus</i>		<i>Dryophis mycterizans</i>	Pujatti (1952)
		<i>Lycodon falavomaculatus</i>	Pujatti (1952)
		<i>Simotes arnensis</i>	Pujatti (1952)
		<i>Thamnophis sirtalis</i>	Read (1950 <i>b</i>)
		<i>Zamenis gracilis</i>	Pujatti (1952)
<i>Centrorhynchus teres</i>		<i>Coluber jugularis</i>	Sharpilo & Sharpilo (1969)
		<i>Coronella austriaca</i>	Sharpilo & Sharpilo (1969)
		<i>Emys orbicularis</i>	Sharpilo & Sharpilo (1969)
		<i>Eremias arguta</i>	Sharpilo & Sharpilo (1969)
		<i>Lacerta agilis</i>	Sharpilo & Sharpilo (1969)
		<i>Lacerta saxicola</i>	Sharpilo & Sharpilo (1969)
		<i>Lacerta taurica</i>	Sharpilo & Sharpilo (1969)
		<i>Natrix natrix</i>	Sharpilo & Sharpilo (1969)
		<i>Natrix tessellata</i>	Sharpilo & Sharpilo (1969)
		<i>Rana ridibunda</i>	Kirbanov (1978 <i>b</i>)
		<i>Vipera ursini</i>	Sharpilo & Sharpilo (1969)
			Golvan & Ormieres (1957)
		<i>Agkistrodon acutus</i>	Schmidt & Kuntz (1969)
		<i>Anolis cristatellus</i>	Acholonu (1976)
<i>Centrorhynchus sp.</i>	<i>Cantatops quadratus</i>	<i>Lycodon subcinctus</i>	Schmidt & Kuntz (1969)
		<i>Natrix sipedon</i>	Ward (1940 <i>b</i>)
		<i>Natrix stolata</i>	Schmidt & Kuntz (1969)
		<i>Psammodynastes pulverulentis</i>	Schmidt & Kuntz (1969)
		<i>Rhacophorus robustus</i>	Schmidt & Kuntz (1969)
		<i>Trimeresurus mucrosquamatus</i>	Schmidt & Kuntz (1969)
		<i>Trimeresurus stejnegeri</i>	Schmidt & Kuntz (1969)
		<i>Hemilepistus pectinatus</i>	Sultanov, Kabilov & Siddikov (1980)
		<i>Melogale moschata subaurantiaca</i>	Schmidt & Kuntz (1969)
		<i>Natrix annularis</i>	Schmidt & Kuntz (1969)
		<i>Paguma larvata taivanus</i>	Schmidt & Kuntz (1969)
		<i>Viverricula indica pallida</i>	Schmidt & Kuntz (1969)
		<i>Rana tigrina rugolosa</i>	Schmidt & Kuntz (1969)
<i>Sphaerirostris lanceoides</i>			
<i>Sphaerirostris pinguis</i>			
<i>Sphaerirostris sp.</i>			

Table 8.1. (cont.)

Species	Intermediate host	Paratenic host	Reference
Family Plagiorhynchidae			
<i>Lueheia inscripta</i>	<i>Periplaneta americana</i>	<i>Anolis cristatellus</i>	Acholonu (1976)
<i>Plagiorhynchus cylindraceus</i>	<i>Armadillidium vulgare</i>		Dollfus & Dalens (1960); Schmidt (1964 <i>b</i>); Schmidt & Olsen (1964); Wanson & Nickol (1975); Dappen & Nickol (1981); Nickol & Dappen (1982)
	<i>Porcellio laevis</i>		Schmidt (1964 <i>b</i>); Schmidt & Olsen (1964)
	<i>Porcellio scaber</i>		Schmidt (1964 <i>b</i>); Schmidt & Olsen (1964)
		<i>Blarina brevicauda</i>	Nickol & Oetinger (1968)
		<i>Eliomys quercinus</i>	Dollfus (1957)
		<i>Erinaceus europaeus</i>	James (1954)
<i>Porrorchis hylae</i>		<i>Boiga trigonata</i>	Gupta & Jain (1975)
		<i>Gekko monarchus</i>	Schmidt & Kuntz (1967 <i>b</i>)
		<i>Hemidactylus frenatus</i>	Schmidt & Kuntz (1967 <i>b</i>)
		<i>Hyla aurea</i>	Johnston & Edmonds (1948)
		<i>Hyla caerulea</i>	Johnston & Edmonds (1948)
		<i>Japalura swinhonis</i>	Schmidt & Kuntz (1967 <i>b</i>)
		<i>Limnodynastes dorsalis</i>	Johnston & Edmonds (1948)
		<i>Psammodynastes pulverulentus</i>	Schmidt & Kuntz (1967 <i>b</i>)
		<i>Rana limnocharis</i>	Schmidt & Kuntz (1967 <i>b</i>)
		<i>Rana tigrina rugulosa</i>	Schmidt & Kuntz (1967 <i>b</i>)
		<i>Trimeresurus stejnegeri</i>	Schmidt & Kuntz (1967 <i>b</i>)
		<i>Zaocys dhumnades</i>	Schmidt & Kuntz (1967 <i>b</i>)
<i>Porrorchis indicus</i>		<i>Lycodon</i> sp.	Das (1957 <i>b</i>)
<i>Porrorchis leibyi</i>		<i>Dinodon rufozonatum</i>	Schmidt & Kuntz (1967 <i>b</i>)
		<i>Gekko monarchus</i>	Schmidt & Kuntz (1967 <i>b</i>)
		<i>Japalura swinhonis</i>	Schmidt & Kuntz (1967 <i>b</i>)
		<i>Natrix stolata</i>	Schmidt & Kuntz (1967 <i>b</i>)
		<i>Rana latouchi</i>	Schmidt & Kuntz (1967 <i>b</i>)

Table 8.1. (cont.)

Species	Intermediate host	Paratenic host	Reference
<i>Porrorchis leiby</i>		<i>Rana tigrina rugulosa</i>	Schmidt & Kuntz (1967b)
		<i>Rhacophorus robustus</i>	Schmidt & Kuntz (1967b)
		<i>Sphenomorphus indicus</i>	Schmidt & Kuntz (1967b)
		<i>Trimeresurus stejnegeri</i>	Schmidt & Kuntz (1967b)
<i>Porrorchis oti</i>		<i>Rana temporaria ornativentris</i>	Yamaguti (1939)
<i>Pseudolueheia pittae</i>		<i>Lycodon subcinctus</i>	Schmidt & Kuntz (1967b)
'Acanthocephaline larvae'	<i>Porcellio</i>		Thompson (1934)
Family Polymorphidae			
<i>Arhythmorhynchus comptus</i>	Freshwater isopods		Atrashkevich (1975a)
<i>Arhythmorhynchus petrochenkoi</i>	<i>Asellus</i> sp.		Atrashkevich (1979a)
<i>Arhythmorhynchus uncinatus</i>		<i>Archosargus probatocephalus</i>	Bullock (1960)
<i>Corynosoma australe</i>		<i>Genypterus chilensis</i>	Vergara & George-Nascimento (1982)
<i>Corynosoma bullosum</i>	<i>Nototheria coriiceps</i>		Edmonds (1955)
<i>Corynosoma clavatum</i>	<i>Platycephalus fuscus</i>		Johnston & Edmonds (1952)
<i>Corynosoma constrictum</i>	<i>Hyaella azteca</i>		Podesta & Holmes (1970)
<i>Corynosoma hadweni</i>		<i>Oncorhynchus nerka</i>	Margolis (1958)
		<i>Osmerus mordax</i>	Van Cleave (1953)
<i>Corynosoma hamanni</i>		<i>Notothenia rossi</i>	Markowski (1971)
		<i>Rhigophila dearborni</i>	Holloway & Bier (1967)
<i>Corynosoma obtuscens</i>		<i>Myctoperca pardalis</i>	Van Cleave (1953)
		<i>Umbrina roncadore</i>	Ward & Winter (1952)
<i>Corynosoma semerme</i>		<i>Acerina cernua</i>	Van Cleave (1953); Dubnitski (1957)
		<i>Anguilla anguilla</i>	Van Cleave (1953)
		<i>Blicca bjoerkna</i>	Van Cleave (1953)
		<i>Clupea harengus</i>	Helle & Valtonen (1981)
		<i>Clupea harengus membras</i>	Van Cleave (1953)
		<i>Coregonus albula</i>	Van Cleave (1953)
		<i>Coregonus fera</i>	Van Cleave (1953)
		<i>Cottus quadricornis</i>	Van Cleave (1953)
		<i>Cottus scorpius</i>	Van Cleave (1953)
		<i>Cyclopterus lumpus</i>	Van Cleave (1953)
		<i>Gadus callorias</i>	Van Cleave (1953)
		<i>Genypterus blacodes</i>	Grabda & Slosarczyk (1981)
		<i>Lota lota</i>	Helle & Valtonen (1981)
		<i>Lota vulgaris</i>	Van Cleave (1953)
		<i>Macruronus novaezelandiae</i>	Grabda & Slosarczyk (1981)

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Table 8.1. (cont.)

Species	Intermediate host	Paratenic host	Reference
<i>Corynosoma semerme</i>		<i>Myoxocephalus quadricornis</i>	Helle & Valtonen (1981)
		<i>Myoxocephalus scorpius</i>	Helle & Valtonen (1981)
		<i>Oncorhynchus nerka</i>	Margolis (1958)
		<i>Onos cumbrinus</i>	Van Cleave (1953)
		<i>Osmerus dentex</i>	Neiland (1962)
		<i>Osmerus eperlanus</i>	Van Cleave (1953); Dubnitski (1957); Jarling (1983)
		<i>Perca fluviatilis</i>	Van Cleave (1953)
		<i>Pleuronectes flesus</i>	Van Cleave (1953)
		<i>Pleuronectes limanda</i>	Van Cleave (1953)
		<i>Pleuronectes platessa</i>	Van Cleave (1953)
		<i>Rhombus maximus</i>	Van Cleave (1953)
		<i>Zoarces viviparus</i>	Van Cleave (1953)
		<i>Osmerus dentex</i>	Neiland (1962)
		<i>Clupea harsangus</i>	Van Cleave (1953); Helle & Valtonen (1981)
		<i>Conger conger</i>	Van Cleave (1953)
		<i>Coregonus fera</i>	Van Cleave (1953)
		<i>Coregonus laveratus</i>	Van Cleave (1953)
		<i>Cottus quadricornis</i>	Van Cleave (1953)
		<i>Cottus scorpius</i>	Van Cleave (1953)
		<i>Cyclopterus lumpus</i>	Van Cleave (1953)
<i>Corynosoma similis</i>		<i>Gadus callarias</i>	Van Cleave (1953)
		<i>Gadus macrocephalus</i>	Van Cleave (1953)
<i>Corynosoma strumosum</i>		<i>Gasterosteus aculeatus</i>	Van Cleave (1953)
		<i>Lepidopsetta bileneata</i>	Van Cleave (1953)
		<i>Leptocottus armatus</i>	Van Cleave (1953)
		<i>Lophius piscatorius</i>	Van Cleave (1953)
		<i>Lota lota</i>	Helle & Valtonen (1981)
		<i>Lota vulgaris</i>	Van Cleave (1953)
		<i>Myoxocephalus quadricornis</i>	Van Cleave (1953); Helle & Valtonen (1981)
		<i>Myoxocephalus scorpius</i>	Helle & Valtonen (1981)
		<i>Oncorhynchus gorbuscha</i>	Margolis (1958)
		<i>Oncorhynchus nerka</i>	Margolis (1958)
		<i>Osmerus dentex</i>	Neiland (1962)
		<i>Osmerus eperlanus</i>	Van Cleave (1953)
		<i>Osmerus lanceolatus</i>	Van Cleave (1953)
		<i>Perca fluviatilis</i>	Van Cleave (1953)
		<i>Platichthyes stellatus</i>	Van Cleave (1953)
		<i>Pleuronectes flesus</i>	Van Cleave (1953)
		<i>Pleuronectes limanda</i>	Van Cleave (1953)
		<i>Rhombus maximus</i>	Van Cleave (1953)
		<i>Sciaena schlegeli</i>	Van Cleave (1953)
		<i>Trachinus draco</i>	Van Cleave (1953)
		<i>Zoarces viviparus</i>	Van Cleave (1953)

Table 8.1. (cont.)

Species	Intermediate host	Paratenic host	Reference
<i>Corynosoma</i> sp.	<i>Homarus americanus</i>		Uzmann (1970)
<i>Filicollis anatis</i>	<i>Asellus aquaticus</i>		Kotelnikov (1954); Styczynska (1958)
	<i>Asellus</i> sp.		Atrashkevich (1979 <i>b</i>)
	<i>Astacus astacus</i>		Golvan (1961)
<i>Filicollis trophimenkoi</i>	<i>Asellus tschaunensis</i>	<i>Hynobius keiserlingii</i>	Atrashkevich (1982)
<i>Hexaglandula mutabilis</i>		<i>Cichlasoma tetracantha</i>	Moravec & Barus (1971)
<i>Polymorphus actuganensis</i>	<i>Gammarus bergi</i>		Chibichenko & Mamytova (1978)
	<i>Gammarus lacustris</i>		Chibichenko & Mamytova (1978)
<i>Polymorphus biziurae</i>	<i>Chevax destructor</i>		Johnston & Edmonds (1948)
<i>Polymorphus botulus</i>	<i>Carcinus moenas</i>		Rayski & Garden (1961); Garden, Rayski & Thom (1964)
	<i>Hyas araneus</i>		Rayski & Garden (1961)
	<i>Pagurus pubescens</i>		Uspenskaja (1960)
<i>Polymorphus contortus</i>	<i>Gammarus lacustris</i>		Denny (1969); Podesta & Holmes (1970)
	<i>Hyaella azteca</i>		Podesta & Holmes (1970)
<i>Polymorphus formosus</i>	<i>Macrobrachium</i> sp.		Schmidt & Kuntz (1967 <i>a</i>)
<i>Polymorphus kenti</i>	<i>Emerita analoga</i>		Reish (1950)
<i>Polymorphus magnus</i>	<i>Gammarus bergi</i>		Chibichenko & Mamytova (1978)
	<i>Gammarus lacustris</i>		Petrochenko (1949); Logachev, Bruskin & Kesten (1961); Klesov & Kovalenko (1967); Chibichenko & Mamytova (1978)
	<i>Gammarus maeoticus</i>		Kovalenko (1960); Klesov & Kovalenko (1967)
	<i>Gammarus pulex</i>		Fotadar, Raina & Dhar (1977); Atrashkevich (1979 <i>b</i>)
	<i>Gammarus wilkitzkii</i>		Atrashkevich (1979 <i>b</i>)
<i>Polymorphus major</i>	<i>Cancer irroratus</i>		Schmidt & MacLean (1978)
<i>Polymorphus marilis</i>	<i>Gammarus lacustris</i>		Denny (1969); Tokeson & Holmes (1982)
<i>Polymorphus minutus</i>	<i>Cambarus affinis</i>		Golvan (1961)
	<i>Carinogammarus roeselii</i>		Scheer (1934)
	<i>Gammarus duebeni</i>		Hynes (1955)
	<i>Gammarus fossarum</i>		Van Maren (1979 <i>a</i>)
	<i>Gammarus lacustris</i>		Hynes (1955); Romanovski (1964); Spencer (1974)

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Table 8.1. (cont.)

Species	Intermediate host	Paratenic host	Reference
<i>Polymorphus minutus</i>	<i>Gammarus limnaeus</i> <i>Gammarus pulex</i>		Schmidt (1964a) Scheer (1934); Florescu (1936); Crompton (1964); Awachie (1967); Butterworth (1969a); Atrashkevich (1979b) Noll (1950)
	<i>Gammarus pulex</i> <i>fossarum</i> <i>Gammarus roeseli</i> <i>Gammarus wilkitzkii</i> <i>Gammarus</i> sp.		Lukacsovics (1959) Atrashkevich (1979b) Hynes & Nicholas (1958); Crompton (1967)
<i>Polymorphus paradoxus</i>	<i>Gammarus lacustris</i>		Bethel & Holmes (1974); Denny (1969)
<i>Polymorphus strumosoides</i>	<i>Gammarus pulex</i>		Atrashkevich (1975b, 1979b)
	<i>Gammarus wilkitzkii</i>		Atrashkevich (1979b)
<i>Polymorphus trochus</i>	<i>Hyaella azteca</i>		Podesta & Holmes (1970)
<i>Polymorphus</i> sp.	<i>Chasmagnathus granulata</i>		Holcman-Spector, Mañe-Garzón & Dei-Cas (1977); Keithly & Ulmer (1965)
<i>Southwellina dimorpha</i>	<i>Pagurus longicarpus</i> <i>Astacus astacus</i>		Reinhard (1944) Lantz (1974)
<i>Southwellina hispida</i>	<i>Procambarus clarkii</i> <i>Macrobrachium</i> sp.		Schmidt (1973a) Schmidt & Kuntz (1967a)
		<i>Cyprinus carassius</i> <i>Elaphe quadrivirgata</i> <i>Fundulus grandis</i> <i>Mogurnda obscura</i> <i>Paralichthys lethostigmus</i> <i>Rana nigromaculata</i> <i>Sciaenops ocellatus</i> <i>Umbrina roncadore</i>	Yamaguti (1935) Yamaguti (1935) Bullock (1957a, b) Yamaguti (1939) Chandler (1935) Yamaguti (1939) Overstreet (1983) Ward & Winter (1952)
<i>Southwellina macracanthus</i>			
Polymorphidae sp.	<i>Orchestoidea trinitatis</i>		Tsimbalyuk, Kulikov, Ardasheva & Tsimbalyuk (1978)
CLASS EOACANTHOCEPHALA			
ORDER GYRACANTHOCEPHALA			
Family Quadrigyridae			
<i>Acanthogyryus dattai</i>	<i>Mesocyclops leuckharti</i>		Sharma & Wattal (1976)
<i>Pallisentis basiri</i>		<i>Trichogaster chuna</i>	Hasan & Qasim (1960)
<i>Pallisentis nagpurensis</i>	<i>Cyclops strenuus</i>	<i>Aplocheilus melastiga</i> <i>Barbus</i> sp.	George & Nadakal (1973) George & Nadakal (1973)

Table 8.1. (cont.)

Species	Intermediate host	Paratenic host	Reference
<i>Pallisentis nagpurensis</i>		<i>Heteropneustes fossilis</i> <i>Macropodus cupanus</i> <i>Ophiocephalus gachua</i> <i>Rana tigrina</i> <i>Wallago attu</i>	George & Nadakal (1984) George & Nadakal (1973) George & Nadakal (1973) George & Nadakal (1984) George & Nadakal (1984)
ORDER NEOECHINORHYNCHIDA			
Family Neoechinorhynchidae			
<i>Atactorhynchus verecundus</i>	<i>Cletocamptus deiresi</i>		Dill (1975)
<i>Neoechinorhynchus cristatus</i>	<i>Cypridopsis helvetica</i>		Uglen (1972b)
<i>Neoechinorhynchus cylindratus</i>	<i>Cypria globula</i>	<i>Ictalurus melas</i> <i>Lepomis gibbosus</i> <i>Lepomis pallidus</i> <i>Fundulus majalis</i> <i>Lucania parva</i> <i>Notropis</i> sp.	Ward (1940a) Samuel, Nickol & Mayes (1976) Samuel, Nickol & Mayes (1976) Ward (1940a) Van Cleave & Bangham (1949) Bullock (1960) Bullock (1960) Hopp (1954)
<i>Neoechinorhynchus doryphorus</i>			
<i>Neoechinorhynchus emydis</i>	<i>Cypria maculata</i> <i>Pleurocerea acuta</i>	<i>Campeloma decusum</i> <i>Campeloma rufum</i> <i>Ceriphasia semicarinata</i>	Whitlock (1939) Hopp (1946, 1954); Lincicome & Whitt (1947) Hopp (1954); Lincicome & Whitt (1947) Merritt & Pratt (1964) Walkey (1962)
<i>Neoechinorhynchus rutili</i>	<i>Cypria turneri</i> ostracods probably the intermediate host; <i>Sialis</i> and <i>Erpobdella</i> are the facultative second intermediate hosts		
<i>Neoechinorhynchus saginatus</i>	<i>Cypridopsis vidua</i>		Uglen & Larson (1969)
<i>Octospinifer macilentus</i>	<i>Cyclocypris serena</i>		Harms (1963, 1965a)
<i>Octospiniferoides chandleri</i>	<i>Cypridopsis vidua</i> <i>Physocypria pustulosa</i>		DeMont & Corkum (1982) DeMont & Corkum (1982)
<i>Paulisentis fractus</i>	<i>Tropocyclops prasinus</i>		Cable & Dill (1967)
<i>Paulisentis missouriensis</i>	<i>Cyclops vernalis</i>		Keppner (1974)
Family Tenuisentidae			
<i>Paratenuisentis ambiguus</i>	<i>Gammarus tigrinus</i>		Samuel & Bullock (1981)
<i>Tenuisentis niloticus</i>		<i>Hydrocyon brevis</i>	Dollfus & Golvan (1956)